Accepted for publication 5 February 2004. Published 9 March 2004.

Evaluation of Soybean Differentials for Their Interaction with *Phytophthora sojae*

A. E. Dorrance and **H. Jia,** Department of Plant Pathology, The Ohio State University, Wooster 44691; and **T. S. Abney,** USDA-ARS, Department of Botany and Plant Pathology, Purdue University, W. Lafayette, IN 47907

Corresponding author: A. E. Dorrance. dorrance.1@osu.edu

Dorrance, A. E., Jia, H., and Abney, T. S. 2004. Evaluation of soybean differentials for their interaction with *Phytophthora sojae*. Online. Plant Health Progress doi:10.1094/PHP-2004-0309-01-RS.

Abstract

Soybean lines, each containing a different resistance gene (*Rps*), are used as differentials to characterize isolates of *Phytophthora sojae* as physiologic races. Surveys in different soybean production regions have used various sets of soybean differentials thought to carry the same *Rps* genes. In some instances, isolates of *P. sojae* have been reported to have different reactions when evaluated in labs using different sets of differentials that were believed to have the same *Rps* gene. The objective of this study was to compare the consistency of racial classification when three different sets of soybean differentials were challenged with a common set of five races of *P. sojae* from Ohio and Indiana. Three soybean differential sets (USDA Soybean Germplasm Collection, The Ohio State University, and USDA-ARS Purdue University) were challenged with *P. sojae* using the hypocotyl inoculation test at OSU and USDA-ARS Purdue. Isolates of races 1, 3, 4, 7, and 25 from Ohio and Indiana had the same reaction on all three sets of soybean differentials for *Rps*1b, *Rps*1c, *Rps*1k, *Rps*3a, *Rps*3b, *Rps*3c, *Rps*6, *Rps*7, and on differentials Harlon, Harosoy 12xx, L59-731, and Union for *Rps*1a. L88-8470 used as a differential for *Rps*1a and L93-3312 used for *Rps*1d did not have the expected response. Isolates of races 4 and 25 from Ohio and Indiana responded differently on differentials with the *Rps*2 gene because this gene was not used previously to characterize races of *P. sojae*. A similar reaction occurred when differentials with *Rps*4 and *Rps*5 were inoculated with isolates of races 1 and 7, respectively. A standardized set of soybean differentials, corresponding to different maturity groups, for thirteen of the fourteen *Rps* genes is recommended.

Introduction

A set of host differentials is comprised of lines or cultivars of a host that have one or more resistance gene(s) to a specific plant pathogen. Host differentials are used in the classification of races or pathotypes of plant pathogenic bacteria, fungi, and nematodes (11). Individual genotypes within a set of differentials may change periodically as additional resistance genes are identified or as pathogen pathotypes change or adapt to resistance genes that are deployed within a region (20).

Phytophthora sojae (M. J. Kaufmann & J. W. Gerdemann) is a host-specific pathogen with more than 55 described races (1,10,12,15,16,23,25,26,27). Recently, the number of virulence genes that have been identified in each pathogen isolate has increased dramatically, which has made the older number classification system cumbersome (10,12,13,17). Hence, pathotypes or virulence formulas are now used to describe virulence patterns based on reactions on sets of differentials (10,12).

Races of *P. sojae* were identified in 1965 using soybean cultivars D60-9647, D60-11082, FC31745, Harrel, and Nansemond (19). Ten years later, a standard set of differentials was adopted by plant pathologists and plant breeders (3,15), which included Harosoy, Harosoy63, Sanga, Mack, Altona, PI 103091, and PI 171442. These differentials allowed researchers to place isolates of *P. sojae* into groups of physiologic races. Subsequently, two sets of soybean differential isolines were developed by backcrossing resistance into the soybean cultivars

Williams (25) and Harosoy (5,6) (Table 1). Currently, there are *Rps* genes that confer resistance to *P. sojae* at eight loci, of which two are comprised of an allelic series (2,4,8). Over the past twenty years, most characterized strains of *P. sojae* races have been based on host differentials that contain *Rps*1a, *Rps*1b, *Rps*1c, *Rps*1d, *Rps*1k, *Rps*3a, *Rps*6, and *Rps*7 (3). Recent surveys have used host differentials with additional *Rps* genes (10,12,13,21,23,26).

Table 1. Soybean differentials originating from the USDA Soybean Germplasm collection (USDA-PGC), The Ohio State University (OSU), and USDA-ARS Purdue University (USDA-P) evaluated with five races of *Phytophthora sojae*.

***Rps* gene**	**Differential[a]**	**Background**	**Source of *Rps* gene**	**Seed source of differential**
rps	Williams	Williams		OSU
*Rps*1a	Harlon	Harosoy	Blackhawk	OSU
	Harosoy 12XX	Harosoy	Blackhawk	OSU
	L59-731 (PI547677)	Harosoy	Blackhawk	USDA-PGC
	Union	Williams	Mukden	USDA-P
	L88-8470 (PI591505)	Williams	Mukden	USDA-PGC
*Rps*1b	Harosoy 13XX	Harosoy	Sanga	OSU
	Harosoy 13XX	Harosoy	Sanga	USDA-P
	L77-1863 (PI547842)	Williams	Harrell	USDA-PGC
*Rps*1c	Williams79	Williams	Lee68	OSU
	L75-3735	Williams	Lee68	USDA-P
	L75-3735 (PI547834)	Williams	Lee68	USDA-PGC
	L77-1727 (PI547841)	Williams	Clark 63 (PI229342)	USDA-PGC
	L85-129 (PI547791)	Harosoy	Higan	USDA-PGC
*Rps*1d	Haro16	Harosoy	PI 103091	USDA-P
	PI 103091	Plant Introduction	PI 103091	OSU
	L99-3312	Williams	PI 103091	USDA-PGC
*Rps*1k	Williams82	Williams	Kingwa	OSU
	Williams82	Williams	Kingwa	USDA-P
	L77-1794 (PI547890)	Williams	Kingwa	USDA-PGC
*Rps*2	L76-1988 (PI547838)	Williams	CNS	USDA-PGC
	L82-1449 (PI547788)	Williams	CNS	USDA-PGC
	L76-1988	Williams	CNS	OSU
*Rps*3a	PI171442	Plant Introduction	PI 171442	USDA-P
	L83-570	Williams	PI 86972-1	OSU
	L83-570 (PI547862)	Williams	PI 86972-1	USDA-PGC
*Rps*3b	L91-8347 (PI591509)	Williams	PI 172901	USDA-PGC
	L89-1541 (PI591507)	Williams	PI 82.312N	USDA-PGC
	L91-8347	Williams	PI 172901	USDA-P
	PRX-146-36	Harosoy		OSU
*Rps*3c	PRX-145-48	Harosoy	PI 340046	OSU
	L92-7857	Williams	PI 340046	USDA-PGC

Table 1 (*continued*). Soybean differentials originating from the USDA Soybean Germplasm collection (USDA-PGC), The Ohio State University (OSU), and USDA-ARS Purdue University (USDA-P) evaluated with five races of *Phytophthora sojae*.

***Rps* gene**	**Differential[a]**	**Background**	**Source of *Rps* gene**	**Seed source of differential**
*Rps*4	L85-2352	Williams	PI 86050	OSU
	L85-2352	Williams	PI 86050	USDA-PGC
*Rps*5	L62-904	Harosoy	PI 91160	USDA-PGC
	L85-3059 (PI547876)	Williams	PI 91160	USDA-PGC
	L85-3059	Williams	PI 91160	OSU
*Rps*6	Haro 62xx	Harosoy		OSU
	L89-1581 (PI591511)	Williams	Altona	USDA-PGC
	L89-1581	Williams	Altona	USDA-P
*Rps*7	Harosoy	Harosoy		OSU
	Harosoy	Harosoy		USDA-P
	L93-3258 (PI591512)	Williams	Harosoy	USDA-PGC
*Rps*1a & *Rps*2	L86-493	Williams		
*Rps*1c & *Rps*2	L81-4352 (PI547856)	Williams	Williams 79 × L76-2013	USDA-PGC

[a] The name of the cultivar or soybean line of each of the differentials along with the accession designation in parenthesis if it is deposited in the USDA Soybean Germplasm Collection in Urbana, IL.

In many cases, soybean cultivars or lines were used as differentials for *P. sojae* prior to the identification of resistance gene(s) in the line (2,15,19). Subsequently, a previously unidentified *Rps* gene or two *Rps* genes were identified in some of these cultivars, i.e., Tracy. For example, Harosoy was regarded as the universal "suscept" in standard differential sets used to characterize races of *P. sojae* during the 1960s and 1970s, but eventually, *P. sojae* isolates were discovered that had a resistant interaction with Harosoy (18). Resistance expressed by Harosoy was conferred by the *Rps*7 gene (2).

Sets of differentials used to classify races of *P. sojae* are not uniform among all researchers. In some instances, the race classification of the same isolate of *P. sojae* differed among labs that were using differentials that were believed to carry the same *Rps* gene. Thus, periodic reassessment of differentials is required to minimize differences between studies as well as to make recommendations for future pathotype evaluations. The objective of this study was to compare the consistency of racial classification when three different sets of the standard soybean differentials were challenged with a common set of five races of *P. sojae* originating from Indiana and Ohio.

The Differential Sets

Sets of the host differentials were obtained from the USDA-ARS Soybean Germplasm Collection (R. Nelson, University of Illinois), USDA-ARS Purdue University and The Ohio State University (Table 1). Seeds of the soybean lines from the Germplasm Collection were increased at The Ohio State University (OSU), Ohio Agricultural Research and Development Center, Wooster, OH. Increased sets of differentials were then used for subsequent evaluations.

The Experiments

Five races of *P. sojae* -- race 1 (*vir* 7), race 3 (1a, 7), race 4 (1a, 1c, 7), race 7 (1a, 3a, 6, 7), and race 25 (1a, 1b, 1c, 1k, 7) -- from both OSU and Purdue were used to evaluate the response of the differentials. The differentials were evaluated at both locations with both sets of isolates using a hypocotyl inoculation technique in laboratory trials (Ohio) and in greenhouse trials (Indiana) (1,4,16,22). The hypocotyl inoculation technique is the preferred method for classifying races of *P. sojae* because there is no interference with partial resistance or field resistance that is expressed in the roots (Figs. 1 to 3). Eight plants of each differential were inoculated with each isolate. At each location, all differentials were evaluated with the same isolate at the same time, but different isolates were evaluated at different times. The reactions were scored as a resistant reaction (R), intermediate (I), and susceptible (S) based on the number of seedlings killed: 0 to 2; 3 to 5; and 6 to 8 dead, respectively. The trials were repeated at each location. The pathotypes were then compared among trials.

A **B**

Fig. 1. (**A**) *Rps* gene expression is evaluated with the hypocotyl inoculation technique where macerated mycelium of *P. sojae* is placed in the hypocotyls of 7- to 10-day-old soybean seedlings. Plants are kept in a humid environment for 15 to 24 hours following inoculation. The plants are evaluated 5 to 10 days following inoculation. (**B**) The presence of a dying or expanded lesion indicates a susceptible or compatible interaction. Resistance response is expressed has a healed wound and healthy seedling.

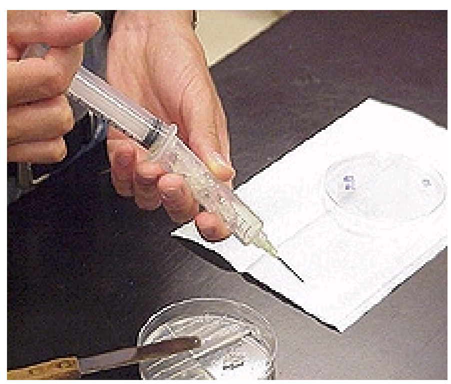
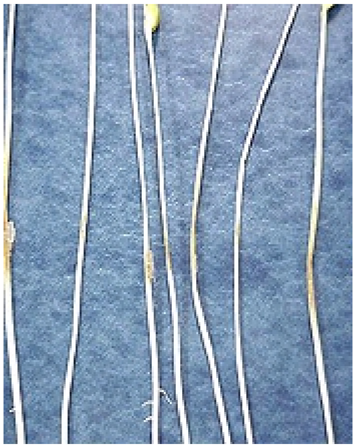


Fig. 2. Inoculum for the hypocotyls inoculation is macerated by placing a *P. sojae* colony from a 7-day-old culture grown on ½-strength lima bean in agar at 15 g/liter into a syringe and passing it through once.


A


B

Fig. 3. (**A**, **B**) For laboratory evaluations of the *Rps* genes, etiolated seedlings are inoculated 7 days after placing on germination paper. The resistance reaction is a necrotic area at the inoculation site; a susceptible interaction is a slowly expanding brown lesion.

Comparison of Same Isolates in Ohio and Indiana

Reactions of the same isolates on differentials in trials at Ohio and Indiana were identical with two exceptions. The differential, Haro16 (*Rps*1d), was resistant to *P. sojae* OHR7 in the Indiana trial but susceptible to this isolate in the Ohio trial. Also, the differential L85-2353 (*Rps*4) was resistant to *P. sojae* INR7 in the Ohio trial but susceptible to this isolate in the Indiana trial (Table 2). Changes in reactions of *P. sojae* isolates on differentials occur over time. Temperature following inoculation, bacterial contamination, and excessive wounding during inoculation alter this response and affect racial classification.

Table 2. Reaction of ten isolates of *P. sojae* representing five races from Ohio and Indiana on three sets of differentials from USDA-ARS Soybean Germplasm Collection, Ohio State/OARDC (OSU), and USDA/Purdue University (Purdue) to determine resistance (R) or susceptibility (S).

Rps gene, Differential[a]	***P. sojae* isolates**									
	Race 1		**Race 3**		**Race 4**		**Race 7**		**Race 25**	
	IN	**OH**	**IN**	**OH**	**IN**	**OH**	**IN**	**OH**	**IN**	**OH**
rps										
Williams	S	S	S	S	S	S	S	S	S	S
***Rps*1a**										
Harlon	R	R	S	S	S	S	S	S	S	S
Harosoy12xx	R	R	S	S	S	S	S	S	S	S
L59-731	R	R	S	S	S	S	S	S	S	S
Union	R	R	S	S	S	S	S	S	S	S
L88-8470	R	R	R	R	S	S	R	R	R	R
***Rps*1b**										
Haro 13XX	R	R	R	R	R	R	R	R	S	S
L77-1863	R	R	R	R	R	R	R	R	S	S
***Rps*1c**										
L75-3735	R	R	R	R	S	S	R	R	S	S
Williams 79	R	R	R	R	S	S	R	R	S	S
L77-1727	R	R	R	R	S	S	R	R	S	S
L85-129	R	R	R	R	S	S	R	R	S	S

Table 2 (*continued*). Reaction of ten isolates of *P. sojae* representing five races from Ohio and Indiana on three sets of differentials from USDA-ARS Soybean Germplasm Collection, Ohio State/OARDC (OSU), and USDA/Purdue University (Purdue) to determine resistance (R) or susceptibility (S).

***Rps* gene, Differential**[a]	***P. sojae* isolates**									
	Race 1		**Race 3**		**Race 4**		**Race 7**		**Race 25**	
	IN	**OH**	**IN**	**OH**	**IN**	**OH**	**IN**	**OH**	**IN**	**OH**
***Rps*1d**										
Haro 16	R	R	R	R	R	R	R	R/S*	R	R
PI103091	R	R	R	R	R	R	R	R	R	R
L99-3312	R	R	S	S	S	S	S	S	S	S
***Rps*1k**										
Williams 82	R	R	R	R	R	R	R	R	S	S
L77-1794	R	R	R	R	R	R	R	R	S	S
***Rps*2**										
L82-1449	R	R	R	I	S	R	S	S	S	R
L76-1988	R	R	R	R	S	R	S	S	S	R
***Rps*3a**										
PI171442	R	R	R	R	R	R	S	S	R	R
L83-570	R	R	R	R	R	R	S	S	R	R
***Rps*3b**										
PRX146-36	R	R	R	R	R	R	R	R	R	R
L91-8347	R	R	R	R	R	R	R	R	R	R
L89-1541	R	R	R	R	R	R	R	R	R	R
***Rps*3c**										
PRX145-48	R	R	R	R	R	R	S	S	R	R
L92-7857	R	R	R	R	R	R	S	S	R	R
***Rps*4**										
L85-2352	S	R	S	R	R	R	R/S*	S	R	R
***Rps*5**										
L62-904	R	R	R	R	R	R	R	S	R	R
L85-3059	R	R	R	R	R	R	R	S	R	R
***Rps*6**										
Haro 62XX	R	R	R	R	R	R	S	S	R	R
L89-1581	R	R	R	R	R	R	S	S	R	R
***Rps*7**										
Harosoy	S	S	S	S	S	S	S	S	S	S
L93-3258	S	S	S	S	S	S	S	S	S	S
***Rps*1a,2**										
L86-493	R	R	R	R	S	R	S	S	S	R
***Rps*1c,2**										
L81-4352	R	R	R	R	S	R	R	R	S	R

* Indicates data from USDA-Purdue compared to Ohio State University where the results were not the same for the same isolate in the two locations.

Comparison of Host Differentials

Races 1, 3, 4, 7, and 25 from both Ohio and Indiana had the expected reaction on all lines in the three sets of differentials used for *Rps*1b, *Rps*1c, *Rps*1k, *Rps*3a, *Rps*3b, *Rps*3c, *Rps*6, and *Rps*7; and on the differentials Harlon, Harosoy 12xx, L59-731, and Union used for *Rps*1a (Table 2). However, several differentials did not have the expected response following inoculation with these races of *P. sojae*. L88-8470, a differential used for *Rps*1a, had resistant reactions to races 3, 7, and 25 whereas the other four differentials used for *Rps*1a were susceptible (Table 2). This indicates that *Rps*1a is not the *Rps* gene(s) present in L99-8470. L99-3312, a differential used for *Rps*1d, was susceptible to races 3, 4, 7, and 25 while the other two differentials for *Rps*1d, Haro 16, and PI 103091 were resistant except Haro 16, inoculated with race OH7 in the Ohio trial. This indicates that L99-3312 has a resistance gene other than *Rps*1d. All of the isolates used in this study caused resistant reactions on differential *Rps*3b. Further evaluations with additional isolates classified as different pathotypes are needed to compare susceptible reactions on *Rps*3b.

Comparison of Isolates from Ohio and Indiana

Differentials that carried the *Rps*2 gene, L86-493 (*Rps*1a and *Rps*2), L81-4352 (*Rps*1c, *Rps*2), L82-1449, and L76-1988 were susceptible to isolates of *P. sojae* races 4 and 25 from Indiana but were resistant to isolates of these same races from Ohio. Differentials with *Rps*5 were resistant to isolates of race 7 from Indiana but susceptible to the isolate of the same race from Ohio. In addition, the differential for *Rps*4, L85-2352, was susceptible to the isolate of race 1 from Indiana but resistant to the isolate of the same race from Ohio. Because *Rps*2, *Rps*4, and *Rps*5 were not used for race classification, these differences are due to the differences in virulence of the isolates and not a reflection of the differentials.

Conclusions

The *P. sojae* populations that are present in the north-central U.S. and Ontario Canada soybean production regions are adapting to many of the commonly deployed *Rps* genes in commercial cultivars (1,7,10,12,13,17). These genes include *Rps*1a, *Rps*1b, *Rps*1c, and *Rps*1k. Future pathotype assessment of the *P. sojae* population within this region should include differentials with as many *Rps* genes as possible to provide the best recommendations about gene deployment.

Based on the results of this study, the soybean differentials presented in Table 3 are recommended for classifying isolates of *P. sojae* against *Rps*1a, *Rps*1b, *Rps*1c, *Rps*1d, *Rps*1k, *Rps*2, *Rps*3a, *Rps*3b, *Rps*3c, *Rps*4, *Rps*5, *Rps*6, and *Rps*7. This set of differentials was chosen based on the consistent reactions in our trials. More than one differential is recommended for each *Rps* gene with two exceptions, *Rps*1k and *Rps*4. Differentials were chosen to cover more than one maturity group, which will allow scientists to maintain their own differentials but also be able to compare their results with others. Differentials with *Rps*1k, *Rps*3a, and *Rps*4 that are in earlier-maturing backgrounds are needed. There are several plant introductions that have been identified recently as novel sources of *Rps* genes, including *Rps*8 in PI399073 (4,9,14). These sources were not evaluated in this study, but they also should be included in differential sets. Periodic reassessment of differentials will be necessary as more *Rps* genes are identified and deployed to ensure that studies can be compared across the regions.

Table 3. Recommended soybean differentials to assess pathotypes (races) of *Phytophthora sojae* based on hypocotyl inoculations with *P. sojae* races 1, 3, 4, 7, and 25.

***Rps* gene**	**Differential**	**Background**	**Maturity group**	**Accession[a]**
rps	Williams	Williams	III	PI 548631
*Rps*1a	Harlon		I	PI 548571
	Harosoy 12xx	Harosoy	II	
	L59-731	Harosoy	II	PI 547677
	Union	Williams	IV	PI 548622
*Rps*1b	Haro13xx	Harosoy	II	
	L77-1863	Williams	III	PI 547842
*Rps*1c	L75-3735	Williams	III	PI 547834
	L85-129	Harosoy	II	PI 547791
*Rps*1d	Haro 16	Harosoy	II	
	PI 103091	Plant Introduction	IV	PI 103091
*Rps*1k	L77-1794	Williams	III	PI 547890
*Rps*2	L82-1449	Harosoy	II	PI 547788
	L76-1988	Williams	III	PI 547838
*Rps*3a	L83-570	Williams/PI 86972-1	III	PI 547862
	PI 171442	Plant Introduction	V	PI 171442
*Rps*3b	L91-8347	Williams	III	PI 591509
	PRX 146-36	Harosoy	II	
*Rps*3c	PRX 145-48	Harosoy	II	
	L92-7857	Williams	III	PI 591510
*Rps*4	L85-2352	Williams	III	PI 547874
*Rps*5	L62-904	Harosoy	II	PI 547764
	L85-3059	Williams	III	PI 547876
*Rps*6	Harosoy 62xx	Harosoy	II	
	L89-1581	Williams	III	PI 591511
*Rps*7	Harosoy	Harosoy	II	
	L93-3258	Williams	III	PI 591512

[a] Accession designation in the USDA-ARS National Plant Germplasm System (24). Other accessions are available through the Ag-Canada Research Station, Harrow, Ontario.

Acknowledgments

We thank S. Berry and B. Bardall for assistance with field increase of seed as well as P. Lipps, M. Ellis, and an anonymous reviewer for their comments on this manuscript. Salaries and research support provided by State and Federal funds appropriated to the Ohio Agricultural Research and Development Center, The Ohio State University. This is a contribution of the Agricultural Research Service, U.S. Department of Agriculture, in cooperation with the Purdue Agricultural Experiment Station, West Lafayette, IN. This research was funded in part by a joint project of the United States Department of Agriculture, the United Soybean Board, and the American Seed Trade Association.

Literature Cited

1. Abney, T. S., Melgar, J. C., Richards, T. L., Scott, D. H., Grogan, J., and Young, J. 1997. New races of *Phytophthora sojae* with *Rps*1-d virulence. Plant Dis. 81:653-655.
2. Anderson, T. R., and Buzzell, R. I. 1992. Inheritance and linkage of the *Rps*7 gene for resistance to Phytophthora root rot of soybean. Plant Dis. 76:958-959.
3. Athow, K. L. 1985. Phytophthora root rot of soybean. Pages 575-581 in: World soybean Res. Con. III: Proceedings. R. Shibles, ed. Westview Press, Boulder, CO.
4. Burnham, K. D., Dorrance, A. E., Francis, D. M., Fioritto, R. J., and St. Martin, S. K. 2003. *Rps*8, A new locus in soybean for resistance to *Phytophthora sojae*. Crop Sci. 43:101-105.
5. Buzzell, R. I., and Anderson, T. R. 1992. Inheritance and race reaction of a new soybean *Rps*1 gene. Plant Dis. 76:600-601.
6. Buzzell, R. I., Anderson, T. R., and Rennie, B. D. 1987. Harosoy *Rps* isolines. Soybean Genet. Newsl. 14:79-81.
7. Cochran, A. J., and Abney, T. S. 1999. *Rps* gene combinations needed to control diverse pathotypes of *Phytophthora sojae*. Phytopathology 89:S104.
8. Diers, B. W., Mansur, L., Imsande, J., and Shoemaker, R. C. 1992. Mapping Phytophthora resistance loci in soybean with restriction fragment length polymorphism markers. Crop Sci. 32:377-383.
9. Dorrance, A. E., and Schmitthenner, A. F. 2000. New sources of resistance to *Phytophthora sojae* in the soybean plant introductions. Plant Dis. 84:1303-1308.
10. Dorrance, A. E., McClure, S. A., and de Silva, A. 2003. Pathogenic diversity of *Phytophthora sojae* in Ohio soybean production fields. Plant Dis. 87:139-146.
11. Flor, H. H. 1971. Current status of the gene-for-gene concept. Ann. Rev. Phytopath. 9:275-296.
12. Kaitany, R. C., Hart, L. P., and Safir, G. R. 2001. Virulence composition of *Phytophthora sojae* in Michigan. Plant Dis. 85:1103-1106.
13. Kurle, J. E., and El Araby, E. M. 2001. Changing composition of *Phytophthora sojae* races in Minnesota soils. Phytopathology 91:S51.
14. Kyle, D. E., Nickell, C. D., Nelson, R. L., and Pedersen, W. L. 1998. Response of soybean accessions from provinces in southern China to *Phytophthora sojae*. Plant Dis. 82:555-559.
15. Laviolette, F. A., and Athow, K. L. 1977. Three new physiologic races of *Phytophthora megasperma* var. *sojae*. Phytopathology 67:267-268.
16. Laviolette, F. A., and Athow, K. L. 1981. Physiologic races of *Phytophthora megasperma* f.sp. *glycinea* in Indiana, 1973-1979. Plant Dis. 65:884-885.
17. Leitz, R.A., Hartman, G.L., Pedersen, W.L. and Nickell, C.D. 2000. Races of *Phytophthora sojae* on soybean in Illinois. Plant Dis. 84:487.
18. Moots, C. K., Nickell, C. D., Gray, L. E. and Lim, S. M. 1983. Reaction of soybean cultivars to 14 races of *Phytophthora megasperma* f.sp. *glycinea*. Plant Dis. 67:764-767.
19. Morgan, F. L., and Hartwig, E. E. 1965. Physiologic specialization in *Phytophthora megasperma* var. *sojae*. Phytopathology 55:1277-1279.
20. Roelfs, A. P., and Martens, J. W. 1988. An international system of nomenclature for *Puccinia graminis* f.sp. *tritici*. Phytopathology 78:526-533.
21. Ryley, M. J., Obst, N. R., Irwin, J. A. G., and Drenth, A. 1998. Changes in the racial composition of *Phytophthora sojae* in Australia between 1979 and 1996. Plant Dis. 82:1048-1054.
22. Schmitthenner, A. F., and Bhat, R. G. 1994. Useful methods for studying *Phytophthora* in the laboratory. OARDC Spec. Circ. No. 143. The Ohio State University, Wooster.
23. Schmitthenner, A. F., Hobe, M., and Bhat, R. G. 1994. *Phytophthora sojae* races in Ohio over a 10-year interval. Plant Dis. 78:269-276.
24. USDA-ARS. 2004. National Plant Germplasm System. Online. Nat. Germplasm Resources Lab., Plant Sci. Inst., Beltsville Agric. Res. Cen., and USDA-ARS.
25. Wagner, R. E., and Bernard, R. L. 1991. Response of Williams isolines to eight races of *Phytophthora megasperma* f.sp. *glycinea*. Soybean Genetics Newsletter 18:236-239.
26. Ward, E. W. B. 1990. The interaction of soya beans with *Phytophthora megasperma* f.sp. *glycinea*: Pathogenicity. Pages 311-327 in: Biological Control of Soil-borne Plant Pathogens. D. Hornby, ed. CAB Int., Wallingford, England.
27. Yang, X. B., Ruff, R. L., Meng, X. Q., and Workneh, F. 1996. Races of *Phytophthora sojae* in Iowa soybean fields. Plant Dis. 80:1418-1420.